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The Paradise Lost of Milia (Grevena, Greece; Late Pliocene, Early Villafranchian, MN15/MN16a): Faunal Composition and Diversity

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Abstract: (1) Background: Over the last decades, important fossil records of Late Pliocene mammals and reptiles have been unearthed in Milia, Grevena (N Greece). This assemblage shows a remarkable composition and diversity, including the partial skeletons of mastodons that reached record-breaking sizes, abundant rhinos—the first occurrence of this species in Greece—and some new species; (2) Methods: We perform a thorough quantitative analysis of the recovered assemblage, presenting the information of the various collection spots in Milia, and calculate various biodiversity indices for each spot; (3) Results: Our research has revealed the vast majority of expected taxa in the assemblage. We argue that the various sub-localities in Milia could be grouped into a larger, composite assemblage representing a short period. We analyze the diversity changes through the various localities in Milia and highlight potential barriers that could affect the distribution of taxa; (4) Conclusions: We re-affirm the Early Villafranchian affinities of the fauna. In particular, Milia should date at MN16a, with a surprising presence of some more archaic, Ruscinian taxa. The fossils of Milia depict a Late Pliocene paradise in the Southern Balkans; a paradise, unfortunately, lost with the onset of the dramatic climate changes of the Quaternary.

Keywords: Villafranchian; Ruscinian; mastodon; turtle; alpha and beta diversity

1. Introduction

The Milia faunal association dates to the earliest part of Villafranchian, which is a period of geologic time (3.5–1.0 Ma) overlapping with the end of the Pliocene and the beginning of the Pleistocene. Dramatic changes in the climate and environment of the Northern Hemisphere mark the transition from the Pliocene to the Pleistocene, the so-called Ice Ages. However, this is a story that starts even earlier, in the period between 3.6 and 2.58 million years, the Piacenzian Stage (Late Pliocene), a stage that also includes the Early Villafranchian. Generally, the climate during the Piacenzian was wetter and warmer (a 2 to 3 °C global mean annual surface temperatures higher than today) than present [1]. In this warm world, however, several short episodes of glaciation took place before the final Northern Hemisphere Glaciation ([2] and references therein). A significant glaciation event in the Northern

Hemisphere occurred approximately at 3.3 Ma (MIS M2), followed by the so-called mid-Piacenzian Warm Period (MPWP; 3.27–2.97 Ma) with a 2 to 3 °C global mean annual surface temperatures higher than today, whereas after 2.7 Ma, the Northern Hemisphere glaciation intensifies ([2] and references therein). Our interest focuses on the MPWP, a period signaled by many as essential for understanding the present and future warming periods of our planet (see [1,2] for reviews and references therein).

Faunal assemblages that survived during this period are commonly grouped in the Early Villafranchian biochronological unit, a concept with a long and complicated history [3]. Milia joins the list of a handful of localities in the Late Pliocene and can offer valuable insights on the fauna composition in southeastern Europe before the Quaternary.

The Milia fossils are scattered in yellow/brownish unconsolidated sand to muddy sand deposits of fluvial origin [4]. The fossils are quite dispersed and span over a distance of more than 20 km around the village of Milia. Practically, the fossils are organized in at least 11 collection spots around Milia, all of which are grouped into larger localities, i.e., MIL 1–11 (Figure 1).

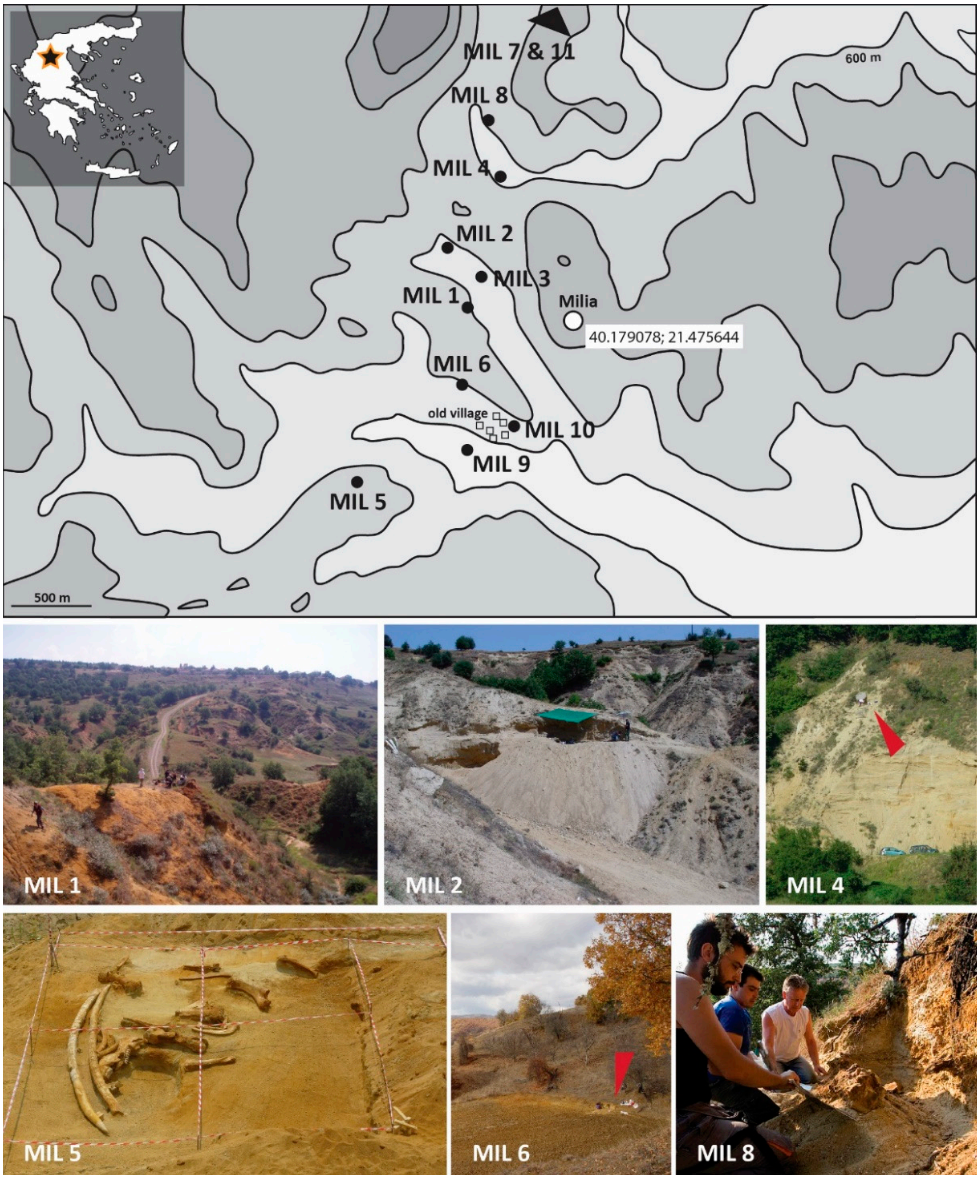

Figure 1. Map with the various localities around the village of Milia, in the Grevena municipality, N Greece, including photographs of the most important localities. Photograph credits: MIL 1, MIL 2, MIL 6: E. Tsoukala; MIL 4, MIL 5: W. van Logchem; MIL 8: H. Wildschut.

Following the first study of the mastodon fossils from Milia [4], the faunal composition of Milia has been under investigation in recent years, with a series of papers describing the various taxa that were recovered and identified in the fossil record: the proboscideans in Tsoukala [4] and Tsoukala and Mol [5], the tapirs, rhinoceroses, and suids in Guérin and Tsoukala [6], the bovids and cervids in Crégut-Bonnoure and Tsoukala [7], carnivores in Tsoukala et al. [8], hipparions in Lazaridis and Tsoukala [9], and turtles in Vlachos and Tsoukala [10]. Based on all these studies mentioned above (and references therein), the composite fauna of Milia can be summarized as follows: (Proboscidea) *Mammut borsoni* and *Anancus arvernensis*; (Perissodactyla) *Tapirus arvernensis arvernensis*, *Stephanorhinus jeanvireti*, *Hipparion* sp. (*H. crassum* group); (Suidae) *Sus arvernensis arvernensis*; (Bovidae) *Grevenobos antiquus*, *Alephis* sp., Bovini indet., *Gazella borbonica*, Antilopinae indet.; (Cervidae) *Croizetoceros ramosus*, Cervidae indet., *Praeelaphus* cf. *lyra*; Ruminantia indet.; (Felidae) *Homotherium crenatidens*; (Ursidae) *Ursus etruscus*, *Agriotherium* sp.; Aves indet.; (Testudines) *Mauremys* sp., *Titanochelon* sp. and *Testudo brevitesta*. Additionally, the presence of a porcupine, *Hystrix* cf. *refossa* can be inferred by a few fossils and some gnawing marks [8].

The emerging Milia fauna allowed for the dating of the locality from a biochronological point of view. The association of *S. jeanvireti*, *T. a. arvernensis* and *S. a. arvernensis* allowed Guérin and Tsoukala [6] to propose an Early Villafranchian (MN16) age. They also notably indicated that the degree of development of the rhino teeth would imply an age that is slightly younger than Vialette (MN16a, 3.14 Ma [11]). The study of the ruminants added taxa with an MN16 distribution, including *C. ramosus* and *G. borbonica*, but also identified taxa like *Alephis* sp. that point out to an older, Ruscinian (MN15), temporal distribution [7]. In particular, they proposed that Milia assemblage dates to the transitional period between MN15 and MN16a, or between the Ruscinian and Early Villafranchian, and that is older than Vialette [7]. The presence of the *Hipparion* in Milia [9] agrees with this expansion to the Ruscinian. Furthermore, the absence of more "modern" faunal elements present in other MN16a assemblages, like *Canis* and *Equus* in Vialette, France [11], and *Mammuthus* in Bulgaria and Romania [12] corroborate the 'archaic' features of Milia assemblage within MN16a.

Therefore, the age correlations provided by the study of mammalian remains and the mixture of species from both MN15 and MN16a biozones raise an intriguing question: is Milia dated indeed in the boundary between the Ruscinian and the Early Villafranchian (MN15/MN16a), or do these fossils represent a time-averaged fauna ranging from MN15 to MN16a? As the Milia fossils are found in several localities around Milia, all in undifferentiated sand deposits with limited stratigraphic information (see below), one might argue that they could represent a composite fauna of at least two faunas: a Ruscinian and a Late Villafranchian one. It is, therefore, necessary to analyze the assemblages of the various sub-localities of Milia in detail and to try to answer this question. In any case, Milia would represent an important assemblage that documents the onset of the Early Villafranchian in southeastern Europe.

The primary objective of this work is to analyze the faunal composition of Milia quantitatively, with a particular emphasis on describing the composition of each of the main collection points in Milia (Figure 1). Up to now, most of the previous works describing the Milia fossils and taxa treated Milia assemblage as coming from a single composite locality. As such, we provide, for the first time, information on each collection spot, its main characteristics and the recovered fauna. Then, we estimate the minimum number of individuals for each locality and Milia as a whole. This information, including the presence/absence data from each locality, is used to produce estimates of alpha and beta diversity across the Milia collections. Finally, we summarize our results and provide testable hypotheses for future research.

2. Materials and Methods

Almost 3300 fossil specimens have been collected in Milia as a result of investigations that lasted over twenty years (1996 to the present day). A total of 40 participants (researchers, students and collaborators) participated in seventeen systematic excavations, resulting in the collected material of large mammals, a micromammal, and turtles. All specimens form part of the LGPUT collection (Laboratory of Geology and Paleontology, School of Geology, Faculty of Sciences, Aristotle University of Thessaloniki, Greece), joined with the acronym MIL (MILia; as LGPUT-MIL). The fossils are currently stored and exhibited in the new Paleontological Exhibition in the village of Milia, Grevena (Figure 2).

Figure 2. The evolving exhibition of Milia, Grevena municipality, N Greece, a landmark locality for the Early Villafranchian and *Mammut borsoni*. (**a**) The previous exhibition, with the two longest pairs of tusks in the world, along with the remaining fossils of the mastodon and other taxa from Milia; (**b**) Detail of the new exhibition, with the tusks in their inferred anatomical position, along with some of the bones of the partial skeletons. Reconstructions of the taxa visible in the photographs are made by R. Bakker, under the supervision of D. Mol. Photographs kindly provided by H. Wildschut.

Upon discovery, one of us (ET) entered each specimen into a digital database in Microsoft Access. The database also included historical (date of collection; collector), anatomical and taxonomic data, updated regularly following the detailed description and study of the various groups over the recent years (see Section 1). This database formed the basis of the analyses herein by the calculation of the Pivot Tables in Microsoft Access and Excel. Preliminary diagrams were created in Microsoft Excel and PAST 3.03 [13], and then further edited in Adobe Illustrator for final presentation purposes. For the analyses herein, the following database records have been excluded as not relevant to this study: two well preserved rhino specimens (a mandible and ulna) from the Priporos site, which is an old sandpit between the Milia and Agios Georgios villages (SGP, 40.171834 N, 021.437836 E) of the former Municipality of Herakleotes [6] and 30 fossilized wood specimens from MIL 1, 5, 6, and broader MIL sites. Rarefaction curves are calculated following Lyman [14] and references therein. The minimum number of individuals is estimated based on Badgley [15], utilizing a range between the Number of Identified Specimens (NISP) and the Minimum Number of Individuals (MNI) counting techniques. *Beta* diversity is based on Koleff et al. [16] and references therein.

3. Localities

For clarity, all points where the fossil specimens have been collected are called "collections", grouped into larger localities, each of which is marked by the systematic excavations by our team (Table 1). The main collection points, where full documented excavations took place, are indicated with a single number (e.g., MIL 1), whereas other collections in their vicinity with the addition of one letter (e.g., MIL 1a).

Table 1. List of the most important fossiliferous collections in Milia, with their local name, coordinates, and Number of Identified Specimens (NISP).

Collections	Local Name	Longitude	Latitude	NISP
Milia-1 (MIL 1)	Lophos (hill)	40.1800861	021.4776389	21
Milia-1a (MIL 1a)	Tsartsarakos	Around Milia-1 site		170
Milia-2 (MIL 2)	Hydragogeio (drilling)	40.1836047	021.4669364	51
Milia-2a (MIL 2a)	-	Around Milia-2 site		192
Milia-3 (MIL 3)	Avraam Koufolakkia	40.181981	021.469151	11
Milia-4 (MIL 4)	Apagorevmeno	40.1872233	021.4694300	6
Milia-4a (MIL 4a)	-	Around Milia-4 site		168
Milia-5 (MIL 5)	Arap Tatsera	40.1696233	021.4600983	200
Milia-5a (MIL 5a)	-	Around Milia-5 site		2196
Milia-6 (MIL 6)	Ambelia	40.1755647	021.4677864	2
Milia-6a (MIL 6a)	Arkoudolakkos	40.17555556	021.46777778	6
Milia-7 (MIL 7)	Kivotos quarry	40.3172733	021.207103	3
Milia-8 (MIL 8)	Kalogeros	40.1913950	021.471023	30
Milia-9 (MIL 9)	Vrissi	40.17166667	021.47222222	5
Milia-9a (MIL 9a)	Mezaria	40.17194444	021.47388889	3
Milia-9b (MIL 9b)	Livadia	Around Milia-9a site		5
Milia-10 (MIL 10)	Agios Nikolaos	40.1728467	021.207861	12
Milia-11 (MIL 11)	Alepotrypes	40.31722222	021.4777836	11
MIL	with no specific locality data			412

The Milia fossils are scattered in the sand deposits of the Aliakmon River (or Haliakmon, the longest river in Greece, 297 km). The various collections (Table 1) are organized in eleven main localities (MIL 1–MIL 11). Among these, the most important are MIL 1, MIL 2, MIL 4, and MIL 5, in which since 1996, systematic excavations have yielded three partial skeletons of *Mammut borsoni*, among other fossils. On a small scale, excavations have also been carried out in the other localities as well, but with fewer specimens. A variety of collection methods were employed in Milia, including standard systematic paleontological excavations, the collection of surface findings during prospection, vertical emergency excavations with the use of ropes and caving techniques, as well as sieving in small (during the systematic excavations and fieldwork) and large-scale (during the works of commercial sandpits). Finally, numerous shepherds, farmers, and locals have accidentally discovered several specimens and donated them to the collection of the Milia Museum.

Unfortunately, there is limited stratigraphic information available linking the various collections of Milia. In all cases, the fossils are found in undifferentiated loose sands stones. Only in a few cases are some sections available (e.g., MIL 4 and MIL 5) where changes in the stratigraphy can be observed, but all our attempts to perform magnetostratigraphy have been unsuccessful. The only available sedimentological analysis is based on the preliminary results reported by Lazaridis et al. [17] from their collection of data from MIL 5 during the excavation of 2007 (note that the 2007 section is no longer available because of the commercial activity on the sandpit). They reported that the fossils in

MIL 5 were found in sand and muddy sand deposits, whereas they also identified a lacustrine layer containing fossil plants and mollusks above the mastodon fossils [17]. The results of the sampling of Lazaridis et al. [17] are not published yet, but the preliminary information of the plant identifications provide further support for a limit of the Pliocene/Pleistocene age for the vertebrate fossils.

3.1. Milia-1 Locality (MIL 1)

The Milia-1 locality (MIL 1) is located across the village of Milia (Figure 1) and was discovered in 1996 by a member the Thessaloniki Aristotle University (AUTH) team at the top of a hill with these typical loose sand-deposits of Aliakmon River that dominate in the area. After a rain, the trochlea of a mastodon humerus was revealed and spotted by the team, leading to the excavation of a partial skeleton of *Mammut borsoni*. Twenty-one specimens were recorded from three systematic excavation campaigns, which revealed the following: in 1997, the skull fragment (maxilla area) with M2 and M3, the two complete upper tusks in a position crosswise and anatomical direction, and the complete right humerus, together with a lower molar of *Grevenobos antiquus*; in 1998, the complete mandible with full dentition, right and left m2, m3, and i2, and the complete right ulna and right tibia; whereas in 1999, thoracic vertebra, the complete left ulna, six ribs, and four indeterminable bone fragments. Species list: *Mammut borsoni*, *Grevenobos antiquus.*

3.2. Milia-1a Collection (MIL 1a)

The collected fossils grouped into the MIL 1a collection spot come from the surroundings of MIL 1, and specifically from the outskirts of Milia village and north of the Tsartsarakos area. It is the area between the MIL 2 and MIL 3 localities. Species list: *Mammut borsoni*, *Hipparion* sp. ("*crassum*" group), *Croizetoceros ramosus*, *Stephanorhinus jeanvireti*, *Grevenobos antiquus*, *Sus arvernensis*, *Testudo brevitesta* and *Homotherium crenatidens.*

3.3. Milia-2 Locality (MIL 2)

The MIL 2 site was also discovered by members of the AUTH team in 2002, in a small ravine between two hills (Figure 1). Four main systematic excavation campaigns took place and brought to light 51 specimens: in 2002, a complete right humerus and left pelvis of a female individual found at the base of the ravine; in 2003, two maxilla fragments with M3 right and M2 left and an almost complete mandible with left and right middle worn m2, m3 of a male individual; in 2004, a cranium fragment with very robust occipital area and condyles, ten ribs, an almost complete thoracic vertebra, spina, arcus and a complete very long left femur; in 2005, six ribs, three thoracic vertebrae, and a lumbar vertebra found in the middle of the right hill. Species list: *Mammut borsoni*, *Grevenobos antiquus*, *Hipparion* sp. ("*crassum*" group), *Gazella borbonica*, *Croizetoceros ramosus*, *Sus arvernensis*, *Stephanorhinus jeanvireti*.

3.4. Milia-2a Collection (MIL 2a)

Outside the systematic excavation area of MIL 2, at least 105 specimens have been collected following prospection, either by the members of the AUTH team or by the locals. From this collection spot, we have been able also to discover the first occurrence of a tapir in Greece, represented by a mandible of a juvenile. Species list: *Mammut borsoni*, *Grevenobos antiquus*, *Hipparion* sp. ("*crassum*" group), *Gazella borbonica*, *Croizetoceros ramosus*, *Sus arvernensis*, *Ursus etruscus*, *Homotherium crenatidens*, *Anancus arvernensis*, *Stephanorhinus jeanvireti*, *Tapirus arvernensis* and *Mauremys* sp.

3.5. Milia-3 Locality (MIL 3)

The MIL 3 site is located on the hillside between the MIL 1 and MIL 2 sites (Figure 1). The most important findings include the complete skull and mandible with the dentition of a rhino, found in 2002 and the skull (holotype) of the large bovid *Grevenobos antiquus,* which was found in 2005. Species list: *Stephanorhinus jeanvireti*, *Grevenobos antiquus*, *Sus arvernensis*, *Croizetoceros ramosus*, *Mammut borsoni*.

3.6. Milia-4 Locality (MIL 4)

The MIL 4 locality is the main vertical outcrop of an old abandoned sandpit, about 25 m high (Figure 1), yielding about 90 specimens. The main findings include a complete *M. borsoni* calcaneum (2005 excavation, at a depth of 12 m from the surface), remains of a *M. borsoni* female individual, with tusks and ribs, associated with a *Grevenobos antiquus* mandible (2010 excavation, at a depth of 19 m from the surface), and the type-specimen of *Testudo brevitesta* (2006 excavation, at a depth of 13 m from the surface). Because of the steep slope, these vertical excavations are often made with the help of ropes and caving harnesses. More fossils found in the broader area, behind MIL 4 and towards the Kokkinia village, were collected in small outcrops by the locals and by the AUTH team; these are grouped under the Milia-4a (MIL 4a) collection spot. Species list: *Mammut borsoni*, *Grevenobos antiquus*, *Testudo brevitesta*. MIL 4a: *Mammut borsoni*, *Stephanorhinus jeanvireti*, *Grevenobos antiquus*, *Hipparion* sp. ("*crassum*" group), *Croizetoceros ramosus*, *Gazella borbonica*, *Testudo brevitesta*.

3.7. Milia-5 Locality (MIL 5)

The MIL 5 site was discovered in 2006 by a crane operator during commercial work in the area (Figure 1). The systematic excavations in 2007 yielded important findings such as the partial skeleton of *M. borsoni* and other fossils found about 14 m below the surface. The excavation followed the paleontological rules with the orientated block of squares, the reference point, the measure of the coordinates and the photographic documentation. The partial skeleton comprises of two cranium fragments, a left maxilla fragment with M2, two complete upper tusks, an almost complete mandible with left and right m2 and m3, a thoracic vertebra spina, 13 ribs, right scapula, right and left humerus and radius, complete right ulna, pisiform, and unciform. The two complete tusks were found in parallel position, but opposite direction (Figure 1): the tip of the one was near the pulp cavity of the other. Thus, we interpreted that the animal died nearby, the tusks were subsequently transported for several meters and formed a barrier that sustained several bones of the skeleton. In addition, right before the entrance to the sandpit of the main excavation of MIL 5, a robust proximal femur with caput and the first and the fourth ribs was discovered and excavated in 2012. This outcrop was named Milia 5′ (MIL 5′). Furthermore, numerous fossils have been collected in the surroundings of MIL 5 by the AUTH team during prospection, by local shepherds as accidental findings, and as the result of the sieving process during the commercial works in the sandpit. The latter works were supervised for three years (2006–2008) by local authorities, yielding abundant fossils (approximately 1100 specimens, including some petrified wood fragments). These findings are grouped under the Milia-5a and 5b collection spots (MIL 5a, MIL 5b). Species list: *Mammut borsoni*, *Grevenobos antiquus*, *Hipparion* sp. ("*crassum*" group), *Gazella borbonica*, *Praeelaphus* cf. *lyra*, *Alephis* sp., *Stephanorhinus jeanvireti*, *Croizetoceros ramosus*, *Sus arvernensis*, *Ursus etruscus*, *Tapirus arvernensis*, *Homotherium crenatidens*, *Agriotherium* sp., *Anancus arvernensis*, *Hystrix* cf. *refossa*, *Testudo brevitesta*, *Titanochelon* sp., *Mauremys* sp.

3.8. Milia-6 Locality (MIL 6)

The Milia-6 collection spot is located in the vineyards between MIL 1 and the old village of Milia (Figure 1) and was discovered during the field plowing. The systematic excavation took place in November 2005 and yielded parts of a tusk of a female Borson's mastodon. In the broader area (Milia-6a, MIL 6a, Arkoudolakkos) few fossils were also collected by a shepherd. Species list: *Mammut borsoni* (MIL 6). MIL 6a: *Stephanorhinus jeanvireti*, *Grevenobos antiquus*, *Mammut borsoni*.

3.9. Milia-7 Locality (MIL 7)

The Milia-7 (MIL 7) collection spot is located at the foothills of an old sandpit, near the village of Kivotos (Figure 1). In 2006, a pelvic fragment with the right acetabulum of a mastodon was excavated. In addition, specimens of a rhino and a cervid were collected by shepherds. Species list: *Mammut borsoni*, *Stephanorhinus jeanvireti*, *Croizetoceros ramosus*.

3.10. Milia-8 Locality (MIL 8)

The Milia 8 site is located at the foot of a hill, towards the village of Kokkinia (Figure 1). In 2008, a well-preserved dorsal part of a rhino skull was excavated. In addition, few specimens of proboscideans and artiodactyls were subsequently discovered. Species list: *Stephanorhinus jeanvireti*, *Mammut borsoni*, *Grevenobos antiquus*, *Anancus arvernensis*.

3.11. Milia-9 Locality (MIL 9)

The Milia-9 (MIL 9) collection spot is located near the old village of Milia, which was abandoned many years ago after a landslide. A local shepherd collected fossils from the Vrissi area. The most important finding is an extremely rare lower deciduous tusk of *Mammut borsoni.* In the broader area of MIL 9, in the areas of Mezaria and Livadia, some bovid and hipparion fossils have been found; both are grouped under Milia-9a (MIL 9a) collection spot. Species list: *Mammut borsoni*, *Stephanorhinus jeanvireti*, *Grevenobos antiquus*, *Hipparion* sp. ("*crassum*" group).

3.12. Milia-10 Locality (MIL 10)

The Milia 10 site is located near the church of the old village of Milia (Figure 1). A local shepherd collected twelve fossils of various animals, including some plastral fragments of a tortoise. Following the delivery of these first specimens, members of the AUTH team visited the place and, through sieving, discovered the remaining fragments of the tortoise plastron. Species list: *Stephanorhinus jeanvireti*, *Mammut borsoni*, *Grevenobos antiquus*, *Hipparion* sp. ("*crassum*" group), *Testudo brevitesta*.

3.13. Milia-11 Locality (MIL 11)

The Milia 11 is located near the village of Kokkinia (Figure 1). Local people collected few fossils of various taxa. Following this information, members of the AUTH team collected a scapula of *M. borsoni*. Species list: *Mammut borsoni*, *Stephanorhinus jeanvireti*, *Hipparion* sp. ("*crassum*" group).

4. Results

4.1. Sample Rarefaction—Do We Have Enough Fossils to Estimate the Faunal Composition of Milia?

At least 3289 fossil specimens have been collected from the various Milia localities, and almost half of them (1472; ~45.8%) could be identified to genus level. As all the identified species belong to different genera, they represent different specific entities as well. The rarefaction analysis (Figure 3a) of the specimens reveals that the amount of identified species rapidly grew in the first years of the research, with a total of 11 identified species during the first 473 identified specimens. During the following ten years, almost 2500 more specimens were added, revealing eight more species that were present in the ancient fauna of Milia. Since 2009, and despite 300 specimens added, no more species were added to the Milia paleofauna. This result better reflects the MIL 5, which not only contains all the identified species from Milia, but also the majority of fossils (Figure 3b). MIL 5 is far more productive than any other locality in Milia, followed by MIL 1, MIL 2, and MIL 4. Our continuous visits to the various localities reveal that only MIL 4 continues to provide new specimens. As we have reached this "plateau" of diversity (Figure 3c), we could assume that we have discovered most of the diversity in the fossil record of Milia; given this rarefaction model, the addition of another species would require the discovery of several hundred more specimens. Therefore, at the level of a compound Milia locality (i.e., composed of all the different localities of Milia), we are quite confident that the analyses herein represent some robust diversity estimates. Based on all the above, we conclude that the preserved analyzed material from the various localities of Milia is enough to allow us to draw greater conclusions on the composition of the Milia paleofauna, and we do not expect any significant sampling bias in the taxonomic composition.

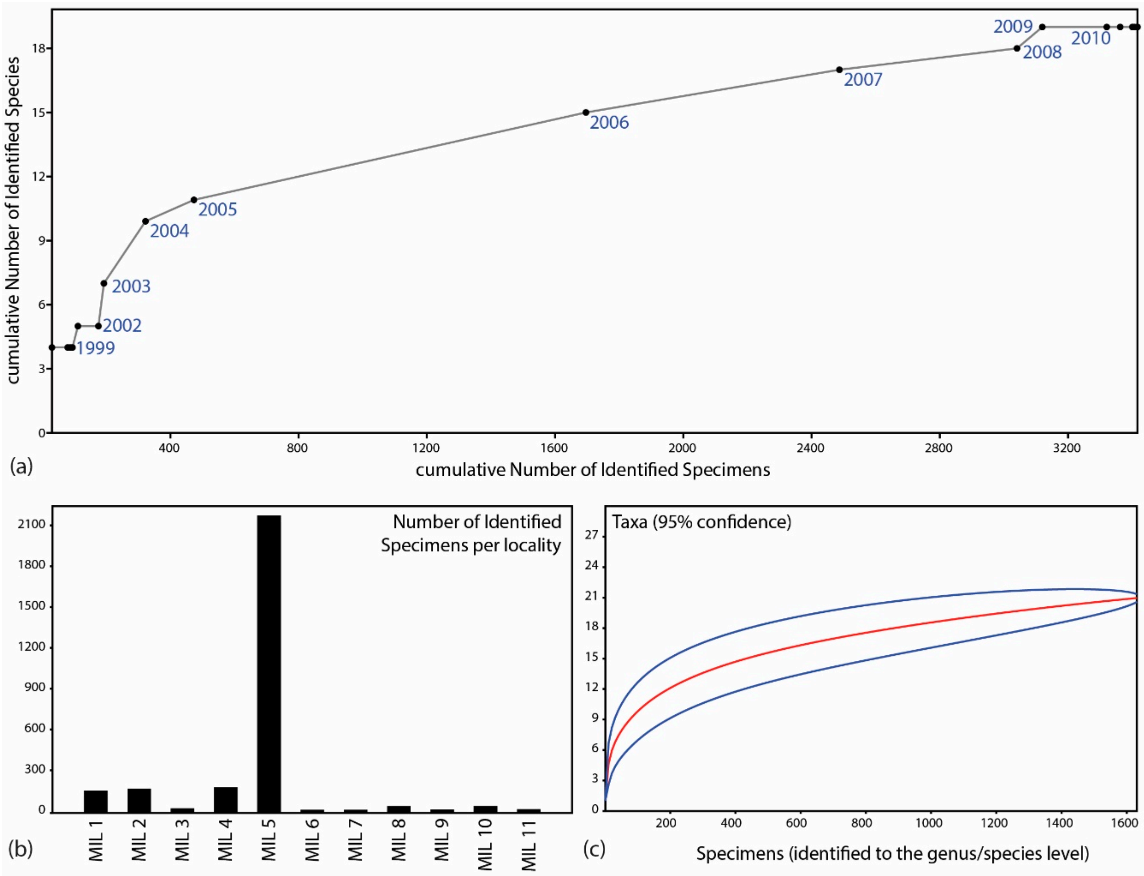

Figure 3. Quantitative analysis of the Milia recovered fauna in locality level. (**a**) the growth on taxic diversity per time in Milia; (**b**) the number of identified specimens per locality; (**c**) sample rarefaction curve of the Milia fossil record.

However, it is clear that there is a collection method bias. As shown above, the collection methods in most localities in Milia include traditional paleontological methods, with exploration, prospecting, and hand-picked collection. Once fossils are discovered, the surrounding sand is usually sieved for additional specimens. MIL 4 is similar, but as it is an open abandoned quarry, the collection is generally carried out on the vertical plane. Finally, the collection in MIL 5 has been additionally made through a large-scale sieving process, during the professional exploitation of the quarry. All-in-all, the fossils in the Milia deposits are indeed widely dispersed, and no evident concentrations of fossils have been encountered so far. However, a much larger volume of sediment has been searched in MIL 5 compared to the rest. As all taxa discovered in Milia are also (or only) discovered in MIL 5, we conclude that the fauna of MIL 5 is representative of Milia in general, and that (regarding taxonomic composition) the various localities can be grouped as one composite fauna without any problems.

4.2. Abundance—How Many Animals Lived in Milia, and Were the Mastodons Dominant?

The majority of the specimens from Milia are found dispersed, without anatomical connection, and fragmented, leading to the hypothesis of a low degree of association (see [15]). Therefore, the appropriate method of estimating the minimum number of individuals would be the NISP (see [15]), where the most abundant element of the skeleton (without taking into account the side, left or right) is used to estimate the MNI^{NISP}. However, there are some cases where some fossils reveal a high degree of association: in MIL 1, MIL 2, MIL 4, MIL 5, and MIL 8, pairs of tusks and/or bones belonging to the same mastodon individual have collected, sometimes with important parts of the skeleton as well (e.g., MIL 1, MIL 5). In all cases, however, the elements are not recovered in an anatomical position and are interpreted as para-autochthonous assemblages. In these cases, according to Badgley [15], the MNI is a more appropriate method for estimating the minimum number of individuals, when the $\mathrm{MNI}^{\mathrm{MNI}}$ is the highest count of one side (left or right) of the most abundant skeletal element. As it is clear that the Milia assemblages contain bones with both a high and low degree of association, both methods have been employed herein to estimate the minimum number of individuals of each species represented in the Milia assemblage.

Our analysis estimates a minimum total of 129^{MNI}–192^{NISP} individuals represented in the fossil record of Milia. As expected, for most of the species, their maximum estimates are found in MIL 5 (Table 2), except for the small-sized tortoise *Testudo brevitesta* that is represented by at least $3/2^{\mathrm{NISP/MNI}}$ in the MIL 4 locality. Taking into account all localities as a whole, the most abundant species (based on the estimates of MNI) are the bovid *Grevenobos antiquus* (from 35^{NISP} to 22^{MNI} minimum individuals), the cervid *Croizetoceros ramosus* (from 32^{NISP} to 20^{MNI} minimum individuals), and the rhino *Stephanorhinus jeanvireti* (from 38^{NISP} to 20^{MNI} minimum individuals) (Table 2). The mastodon of Milia, *Mammut borsoni*, follows with 32^{NISP} to 12^{MNI} minimum individuals and *Hipparion* sp. with 19^{NISP} to 14^{MNI} minimum individuals. The remaining taxa are much less represented in the Milia paleofauna with estimates of minimum individuals that range between 2 and 9 (e.g., *Agriotherium* sp., *A. arvernensis*, *Gazella borbonica*, *Testudo brevitesta*, *Sus a. arvernensis*, *Tapirus a. arvernensis*, *Mauremys* sp., *Ursus etruscus*, *Homotherium crenatidens*) or just with solitary individuals (e.g., *Alephis* sp., *Hystrix* cf. *refossa*, *Praeelaphus* cf. *lyra*, *Titanochelon* sp. and Aves).

Table 2. Estimation of the minimum number of individuals per locality based on both NISP/MNI counting techniques. See Supplementary Materials for raw data.

Taxa	MIL 5	MIL 9	MIL 10	MIL 6	MIL 1	MIL 3	MIL2	MIL 4	MIL 8	MIL 7	MIL 11	Totals
M. borsoni	**10/8**	1/1	1/1	3/2	4/2	1/1	2/2	5/2	2/1	1/1	2/1	**32/12**
A. arvernensis	**1**/1	-	-	-	-	-	1/1	-	1/1	-	-	**3/3**
T. a. arvernensis	1/1	-	-	-	-	-	1/1	-	-	-	-	**2/2**
S. jeanvireti	**19/6**	1/1	1/1	2/1	2/1	2/1	4/3	4/3	1/1	1/1	1/1	**38/20**
Hipparion sp.	**8/6**	3/1	1/1	-	2/1	-	3/3	1/1	-	-	1/1	**19/14**
S. a. arvernensis	**1/1**	-	-	-	1/1	1/1	2/2	-	-	-	-	**5/5**
G. antiquus	**20/10**	2/2	2/1	1/1	3/2	1/1	2/2	3/2	1/1	-	-	**35/22**
Alephis sp.	**1/1**	-	-	-	-	-	-	-	-	-	-	**1/1**
G. borbonica	**5/3**	-	-	-	-	-	2/2	1/1	-	-	-	**8/6**
C. ramosus	**23/13**	-	-	-	2/2	1/1	3/2	2/1	-	1/1	-	**32/20**
P. cf. *lyra*	**1/1**	-	-	-	-	-	-	-	-	-	-	**1/1**
H. crenatidens	1/1	-	-	-	1/1	-	1/1	-	-	-	-	**3/3**
Ursus etruscus	**1/1**	-	-	-	-	-	1/1	-	-	-	-	**2/2**
Agriotherium sp.	**2/2**	-	-	-	-	-	-	-	-	-	-	**2/2**
H. cf. *refossa*	**1/1**	-	-	-	-	-	-	-	-	-		**1/1**
Aves	**1/1**	-	-	-	-	-	-	-	-	-	-	**1/1**
Mauremys sp.	**3/3**	-	-	-	-	-	1/1	-	-	-	-	**4/4**
Titanochelon sp.	**1/1**	-	-	-	-	-	-	-	-	-	-	**1/1**
T. brevitesta	2/2	-	1/1	-	1/1	-	1/1	**3/2**	-	-	-	**8/7**
NISP/MNI	**102/56**	**7/5**	**6/4**	**6/4**	**16/11**	**6/5**	**24/22**	**19/12**	**5/4**	**3/3**	**4/3**	**192/129**

MNI, Minimum Number of Individuals; NISP, Number of Identified Specimens; bold denotes the maxima of each species across the localities.

If one uses the $\mathrm{MNI}^{\mathrm{NISP}}$ as an estimate, then *C. ramosus*, *G. antiquus*, and *S. jeanvireti* dominate over the mastodon. The estimates of individuals per locality provide interesting conclusions as well. Estimates from MIL 5 are mostly similar to the general ones, so they will not be repeated. Most of the remaining localities contain only solitary individuals, except MIL 1 with at least two individuals of *G. antiquus*, MIL 2 with possibly more than two individuals for most taxa, MIL 4 with more than 3 individuals of *S. jeanvireti* and 2 of *T. brevitesta*, and finally the possibility of having more than one individual of *M. borsoni* in MIL 1 and MIL 6. As these estimates are minima, the ratios cannot be calculated [14], but overall the dominance of some species is evident.

4.3. Alpha and Beta Diversity—Which Is the Most Diverse Locality in Milia?

The presence/absence of the species and their abundance per locality allow for the first estimation of the within-habitat diversity or alpha diversity [18]. Apparently, there is no doubt that the MIL 5 assemblage is the richest, a conclusion that is observed in all relevant diversity indices in Table 3, therefore we will focus mostly on the rest. It is interesting to note that the alpha diversity of the locality is not tightly related to the abundance of fossils. For example, although MIL 4 is the second most prolific locality in Milia, its alpha diversity is much lower than in MIL 2, a locality that gave much fewer fossils (Table 3). The remaining localities are much poorer, again with no apparent correlation between fossil abundance and species richness (Table 3). However, as we have seen above, there is a significant difference between the number of specimens found in MIL 5 compared to the other localities. Although there is no doubt that MIL 5 is the richest locality, one might argue that this is biased. Of course, rarefaction analysis showed that this bias would not probably affect the faunal composition, but of course, better sampling would most certainly affect the alpha diversity of the various localities. The calculation of Menhinick's and Margalef's richness indices ([19] and references therein) reveal that with higher sampling the picture could be completely different (Table 3). Under Menhinick's richness index (Table 3), MIL 2 could be the richest locality, and the rest have reached or even surpassed MIL 5. Under Margalef's richness index (Table 3) however, MIL 5 is still more productive than most. On the other hand, MIL 6 and MIL 11 are among the poorest localities in all analyses. By being the poorest, these localities show the highest dominance (Table 3) and, as expected, MIL 5 shows the evenest composition (Table 3).

Table 3. Various biodiversity indices based on the presence/absence of taxa in the various localities of Milia. Localities are sorted from the southernmost (MIL 5) to the northernmost one (MIL 11). See [19] for definitions of the indices and text for further details. Cells are colored from lowest (light grey) to highest (dark grey) value. See Supplementary Materials for raw data.

Diversity Indices	MIL5	MIL9	MIL10	MIL6	MIL1	MIL3	MIL2	MIL4	MIL8	MIL7	MIL11
Richness S	19	4	5	3	7	5	13	7	4	3	3
Chao-1	34	5.5	15	3.5	8.5	15	15.5	7.75	10	6	6
Menhinick	2.394	1.789	2.236	1.5	2.214	2.236	2.772	2.021	2	1.732	1.732
Margalef	4.345	1.864	2.485	1.443	2.606	2.485	3.882	2.415	2.164	1.82	1.82
Dominance	0.1111	0.28	0.2	0.375	0.16	0.2	0.09091	0.1667	0.25	0.3333	0.3333
Simpson	0.8889	0.72	0.8	0.625	0.84	0.8	0.9091	0.8333	0.75	0.6667	0.6667
Evenness	0.6376	0.9473	1	0.9428	0.9425	1	0.9152	0.9211	1	1	1

The various assemblages of Milia constitute an ideal case for studying changes of beta diversity, or changes in species composition between these local assemblages ([16,17] and references therein). The various localities are more-or-less distributed along the same hypothetical line as follows (from south to north; number of arrows indicates relative distance): MIL 5 >> MIL 9 > MIL 10 >> MIL 6 >> MIL 1 > MIL 3 > MIL 2 >> MIL 4 >> MIL 8 >>> MIL 7 >>> MIL11 (see Figures 1 and 4). In total, the fossils from Milia span across a line of more than 20 km.

Across this line, we can observe significant changes in beta diversity (Table 4), based on many indices redefined by Koleff [16] (and references therein) and implemented in PAST [13,19]. In general, the diversity changes drastically from MIL 5 to the rest, as the nearby localities MIL 9, MIL 10 and MIL 6 are among the poorest and less diverse. There are few changes in diversity between the nearby localities MIL 1 and MIL 3, but then again significant changes from MIL 2 to MIL 8. Interestingly, although being quite remote, the differences between MIL 7 and MIL 11 from the rest are fewer than expected.

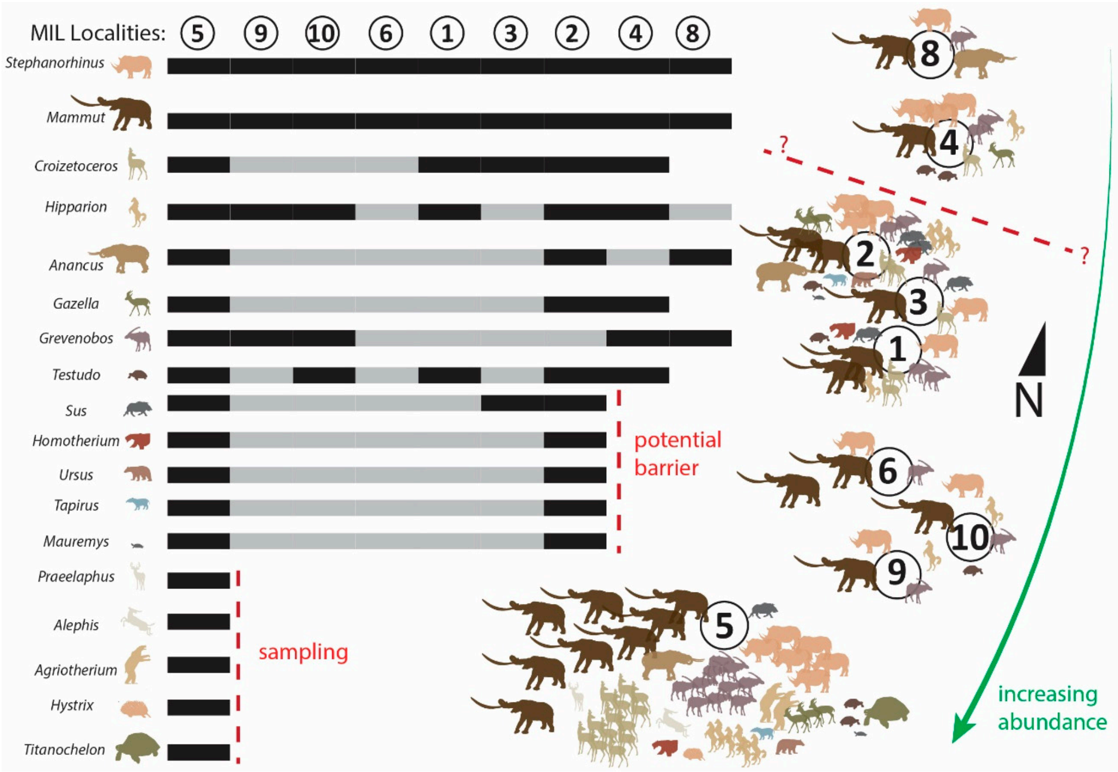

Figure 4. The distribution of taxa across the various localities of Milia (black: presence; grey: absence), and visual representation of their abundance based on the minimum number of individuals. The distributional analysis revealed the presence of two barriers, one between MIL 5 and the rest, probably because of sampling bias and a possible barrier between MIL 2 and MIL 4 that could be related to paleoenvironmental differences (see text for further details). Silhouettes of *Mammut*, *Anancus*, *Homotherium*, and *Grevenobos* are based on the drawings of R. Bakker (under the supervision of D. Mol); the rest are re-drawn and simplified based on open access online silhouettes.

Table 4. Changes in beta diversity across the Milia localities (see text for further explanation). Each column indicates the differences between the locality in the column and the previous locality (rounded to two decimal digits). Abbreviations of the indices: Co, Cody; Ha, Harrison-2; Wh, Whittaker; Wi, Williams; WS, Wilson-Shmida. See Koleff [16] for definition and text for further details. Cells are colored from lowest (light grey) to highest (dark grey) value. See Supplementary Materials for raw data.

	MIL5	MIL9	MIL10	MIL6	MIL1	MIL3	MIL2	MIL4	MIL8	MIL7	MIL11
Wh	0	0.65	0.11	0.25	0.40	0.17	0.44	0.30	0.45	0.43	0.33
Co	0	7.50	0.50	1.00	2.00	1.00	4.00	3.00	2.50	1.50	1.00
WS	0	0.65	0.11	0.25	0.40	0.17	0.44	0.30	0.45	0.43	0.33
Ha2	0	0	0	0	0	0	0	0	0.14	0.25	0.33
Wi	0	0	0	0	0	0	0	0	0.13	0.20	0.25

The indices calculated in Table 4 work by comparing the localities as pairs of quadrats, and especially based on the species present in each one of the localities alone, on in both (a, b, c components in Koleff [16]). When all components are considered (e.g., Whittaker index; Table 4), we notice important changes after the MIL 2 locality. When the importance of the species in common between each of the two localities is down weighted compared to all components (Harrison-2, Williams indices; Table 4), the most important changes in diversity are noted after the MIL 8 locality, where diversity drops. The heterogeneity among the various localities is evident in the Cody index (Table 4; that does not take into account the species in common between the localities), notably between MIL 5 and MIL 9 (sampling bias), as well as between MIL 3–MIL 2–MIL 4–MIL

8. Therefore, without further considering the changes between MIL 5 and the rest that are obviously due to sampling factors, it seems that there are some changes in the diversity in the central-northern parts of the study area that might require further analysis.

Based on the recovered distribution (Figure 4), it appears that *M. borsoni*, *S. jeanvireti*, and the *Hipparion* have been distributed in the entire area, followed by *G. antiquus* that also had an extensive distribution, except in the more remote MIL 7 and MIL 11 localities. The first potential barrier is right after MIL 5, as several species are only found in this locality (*Agriotherium* sp., *Alephis* sp., *P.* cf. *lyra*, Aves, *Titanochelon* sp.); this barrier, however, is most probably the result of sampling bias. A second potential barrier, which is most promising for our interpretations, is located between MIL 2 and MIL 4. After their presence in MIL 2 (that is an important and relatively diverse locality; see above), some species do not extend to the northern parts, including *H. crenatidens*, *S. arvernensis*, *T. arvernensis*, *U. etruscus*, and *Mauremys* sp. (aquatic turtle). Based on the available fossil record, few taxa only cross this boundary: those mentioned above as having a widespread distribution (mastodon, rhino, hipparion, bovid), the gazelle, and the small testudinid. Among the taxa that do not extend beyond the MIL 4, the suid, tapir, and terrapin, are animals that most probably indicate the presence of water bodies, such as lakes and rivers. It is clear that this potential barrier needs to be confirmed by further sampling in MIL 2 and MIL 4, but provides an initial hypothesis of some ecological differences between the localities. This hypothesis could be formulated as having significant water bodies in the area defined from MIL 5 to MIL 2, which did not extend in the past to MIL 4 and beyond. Although more rare and solitary, the absence of the hypercarnivore *Homotherium* beyond MIL 2 would be in accordance with this hypothesis, as the carnivores would lurk in areas with water bodies and higher concentrations of prey. In any case, because of the low number of fossils in these localities compared to MIL 5, more specimens would help validate the existence of this potential barrier and test a possible taphonomical/sampling bias.

5. Concluding Remarks

Paleontological investigations in the area of Milia during the last 20 years have brought to light more than 3200 fossil specimens of mammals, birds, and turtles of at least 19 different taxa. Based on previous systematic works (see Introduction), we are now able to summarize the taxonomic catalog of Milia and further analyze it in the regional context within the sub-localities of Milia. Although the taxonomic composition and species richness vary among the various collections of Milia, the wide distribution of *Stephanorhinus jeanvireti*, *Mammut borsoni*, *Croizetoceros ramosus*, *Hipparion* sp. (*H. crassum* group), *Anancus arvernensis*, *Gazella borbonica*, *Grevenobos antiquus* and *Testudo brevitesta* allow us to correlate them clearly. The presence of partial skeletons in several localities, pairs of tusks and associated specimens indicate that there is a considerable degree of association between the recovered fossils. At the same time, there is also clear evidence of moderate fluvial transport and the further modification of the original assemblages. Thus, we can argue with considerable evidence that the collections made in the various localities around Milia represent a single assemblage; as the majority of the localities are surface collections of small extension, both horizontally and vertically, we conclude that most likely the Milia assemblage had a short temporal distribution. In any case, this conclusion should be backed by more stratigraphical, sedimentological, and chronological data in the ongoing research in Grevena.

The abundance of the rhino *S. jeanvireti* and the mastodon *M. borsoni* confirms the MN16 character of the Milia fauna, further corroborated by the solitary findings of *Tapirus a. arvernensis* and *Sus a. arvernensis* (Figure 4). The presence of *Agriotherium* would instead constrain the age of the Milia assemblage to the MN16a; indeed, the Milia fauna is quite similar to Vialette (France) and Triversa (Italy) faunas. Interestingly, the presence of *Hipparion* sp. and *Alephis* sp. indicate an older MN15 temporal distribution as these taxa are typically found up to MN15 (e.g., Perpignan, France)—still, Milia is undoubtedly different from Perpignan, as the rhino, suid, cervid, bear, and tapir belong to different species or subspecies compared to the French locality.

As far as the estimation of the age of the Milia fauna from a biochronological point of view is concerned, we strongly re-affirm the Early Villafranchian (MN16) affinities of Milia and we even suggest that it represents an MN16a fauna. The presence of Ruscinian (MN15) elements in the assemblage is intriguing and based on the available evidence can be explained with the extended survival of Ruscinian taxa in Greece, either in the boundary between the Ruscinian and the Early Villafranchian or to the earliest Villafranchian. In any case, and from a biochronological point of view, Milia should be older than Vialette (<3.14 Ma), in agreement with Crégut-Bonnoure and Tsoukala [7]. However, we would like to point out that the refinement of the age estimation of Milia is based on three taxa identified only up to the genus level. Although for our conclusion herein this level of identification is enough, the discovery of more specimens belonging to these taxa that could lead to a more detailed identification would be of paramount importance for the ongoing research in Milia.

Milia joins a handful of Late Pliocene localities that allow documenting the onset of the Villafranchian, including Vialette (MN16a) and Etouaires (MN16b) from France, Triversa (MN16a) and Montopoli (MN16b) from Italy, Villaroya (MN16) from Spain, and Hajnacka (MN16) from Slovakia ([3,11,20,21] and references therein). These localities demonstrate the latest chapters of the long evolutionary history of successful and widespread species such as *Mammut borsoni*, *Stephanorhinus jeanvireti* and *Tapirus arvernensis* that became extinct at the end of the Pliocene. Milia and the localities mentioned above also provide evidence of the typical Late Neogene faunas of Europe that changed drastically in the Pleistocene. In Milia, we have fantastic evidence of the favorable conditions that existed in the Late Pliocene, as several taxa are found to reach larger-than-expected and even record-breaking sizes. Of course, the mastodon *M. borsoni* is, beyond any doubt, a true giant surviving in Milia, having the longest tusks discovered so far that reach 5 m in length. However, most of the other species known from Milia also reached large sizes: the dimensions of the rhino bones are closer to the highest values of this species and in some cases exceed them, whereas the tapir is among the largest as well [6]; the turtles were also large, with a giant tortoise, a robust small-sized tortoise and probably the largest member of *Mauremys* known [10]. Therefore, the Milia fossils could provide valuable evidence on the life history of these species, and suggest the presence of exceptionally favorable conditions in Milia at the beginning of the Villafranchian.

The quantitative analysis herein shows that sampling in Milia is sufficient to provide some robust estimates of the species richness in the area. In other words, it seems that our investigations have already led to the discovery of the vast majority of the taxa represented in the fossil record of Milia. Besides the identification of well-known and widespread taxa, we have been able also to discover some new taxa, including the bovid *Grevenobos antiquus* [7] and the tortoise *Testudo brevitesta* [10]. The most abundant and widespread taxa were the rhino *S. jeanvireti*, the bovid *G. antiquus*, and the cervid *C. ramosus*, followed closely by the mastodon *M. borsoni*, together tallying up to a total of at least 74–137 individuals. The remaining species were less frequent with only a handful or isolated occurrences. Overall, we estimate that the Milia fossils represent at least 129 to 192 different individuals.

The analysis of alpha and beta diversity confirmed the importance of the MIL 5 locality, the richest and most diverse collection in Milia. However, our analysis highlights for the first time that future research should focus on both MIL 2 and MIL 4 localities. These localities show a significant potential of providing an even more diverse record than they already have. Additionally, the analysis of beta diversity suggests a potential barrier between these two localities (currently divided by the hill of the Milia village), as several species that are more adapted to wet environments (*Sus*, *Tapirus*, and *Mauremys*) and two carnivores (*Homotherium* and *Ursus*) fail to cross this potential barrier. Further sampling in these localities would be of paramount importance to help identify potential biogeographical barriers in the composite Milia assemblage and to exclude other types of bias (taphonomical, sampling) that could alter our interpretations. Our work further identifies the area south of MIL 5 as having enormous potential for future discoveries because of the following observations: (a) the various collections are placed, almost, on a line of north-to-south orientation; (b) MIL 5 is the southernmost, richest and most diverse locality; (c) even with the sampling bias of MIL 5, the abundance (seen as minimum number of individuals) increases towards the south. Consequently, future research should focus on the discovery of more fossil collection points towards the south. Additionally, based on the first results expressed herein, future research in Milia should also focus on detailed taphonomical analyses of the fossils.

The abundance and richness of the fossil record summarized herein place Milia as the richest Pliocene locality in Greece and among the richest in Europe, dating back to a crucial period for the faunal evolution in the Palearctic region. Although this work focuses on what is going on within the Milia assemblage, we hope that it culminates an initial period of research of this important paleontological paradise. During this initial period, we have been able to confidently identify the taxic diversity in Milia (see previous works in Introduction) and analyze the diversity of this composite assemblage in quantitative terms (this work). Several of the questions raised above will set the basis for our future research in Milia. We also hope that this basis will serve others to include the Milia assemblage in future discussions surrounding the faunal changes during the Early Villafranchian and Quaternary. We anticipate that the fossil record of Milia will hold a significant place in these discussions and could be considered as a reference point for the MN16a biozone in southeastern Europe. It should also be recognized as the best-preserved fossil record of the mastodon *Mammut borsoni*, a species with a broad distribution temporally and geographically, but never known by such complete fossils that allow detailed documentation of its anatomy.

Shortly after their co-occurrence in Milia, the giants of the Early Villafranchian, including *M. borsoni*, and *S. jeanvireti*, survived a bit longer but never crossed to the Quaternary. Instead, *A. arvernensis*, *G. borbonica*, *C. ramosus*, *H. crenatidens*, and *Titanochelon* managed to survive a little more at the beginning of the Quaternary before they became, eventually, extinct. Milia paints with vivid colors the calmness before the Quaternary "storm" that brought dramatic and shocking faunal and climate changes. As its unique fossils indicate, around 3 Ma Milia was a paradise for these animals without water or food shortage, allowing them to reach record-breaking sizes and a remarkable diversity—a paradise lost following the climate changes in the Quaternary.

Supplementary Materials: The following are available online at http://www.mdpi.com/2571-550X/1/2/13/s1. File S1: spreadsheet containing the quantitative information used for the analyses therein.

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References

1. Salzmann, U.; Williams, M.; Haywood, A.M.; Johnson, A.L.; Kender, S.; Zalasiewicz, J. Climate and environment of a Pliocene warm world. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **2011**, *309*, 1–8. [CrossRef]
2. De Schepper, S.; Gibbard, P.L.; Salzmann, U.; Ehlers, J. A global synthesis of the marine and terrestrial evidence for glaciation during the Pliocene Epoch. *Earth-Sci. Rev.* **2014**, *135*, 83–102. [CrossRef]
3. Rook, L.; Martínez-Navarro, B. Villafranchian: The long story of a Plio-Pleistocene European large mammal biochronologic unit. *Quat. Int.* **2010**, *219*, 134–144. [CrossRef]
4. Tsoukala, E. Remains of a Pliocene *Mammut borsoni* (Hays, 1834) (Proboscidea, Mammalia) from Milia (Grevena, W. Macedonia, Greece). *Ann. Paléontol.* **2000**, *86*, 165–191. [CrossRef]

5. Tsoukala, E.; Mol, D. The Proboscidea of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). *Quat. Int.* **2016**, *406*, 2–24. [CrossRef]
6. Guérin, C.; Tsoukala, E. The Tapiridae, Rhinocerotidae and Suidae (Mammalia) of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). *Geodiversitas* **2013**, *35*, 447–489. [CrossRef]
7. Crégut-Bonnoure, E.; Tsoukala, E. The Late Pliocene Bovidae and Cervidae (Mammalia) of Milia (Grevena, Macedonia, Greece). *Quat. Int.* **2017**, *445*, 215–249. [CrossRef]
8. Tsoukala, E.; van Logchem, W.; Lazaridis, G.; Mol, D. Carnivores of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). In *Abstract Book of the VIth International Conference on Mammoths and Their Relatives, Grevena and Siatista, Greece, May 2014*; Scientific Annals; School of Geology, Aristotle University: Thessaloniki, Greece, 2014; Volume 102, pp. 6–7.
9. Lazaridis, G.; Tsoukala, E. Short note on the Equidae of the Early Villafranchian site of Milia (Grevena, Macedonia, Greece). In *Abstract Book of the VIth International Conference on Mammoths and Their Relatives, Grevena and Siatista, Greece, May 2014*; Scientific Annals; School of Geology, Aristotle University: Thessaloniki, Greece, 2014; Volume 102, p. 8.
10. Vlachos, E.; Tsoukala, E. The diverse fossil chelonians from Milia (Late Pliocene, Grevena, Greece) with a new species of *Testudo* Linnaeus, 1758 (Testudines: Testudinidae). *Pap. Palaeontol.* **2016**, *2*, 71–86. [CrossRef]
11. Lacombat, F.; Abbazzi, L.; Ferretti, M.P.; Martínez-Navarro, B.; Moulle, P.E.; Palombo, M.R.; Rook, L.; Turner, A.; Valli, A.M.F. New data on the Early Villafranchian fauna from Vialette (Haute-Loire, France) based on the collection of the Crozatier Museum (Le Puy-en-Velay, Haute-Loire, France). *Quat. Int.* **2008**, *179*, 64–71. [CrossRef]
12. Markov, G.N.; Spassov, N. Primitive mammoths from Northeast Bulgaria in the context of the earliest mammoth migrations in Europe. In *Advances in Vertebrate Paleontology 'Hen to Panta'*; Petculescu, A., Stiuca, E., Eds.; Romanian Academy Institute of Speleology 'Emil Racovita': Bucharest, Romania, 2003; pp. 53–58.
13. Hammer, O.; Harper, D.A.T.; Ryan, P.D. PAST (Paleontological Statistics) Version 3.03. 2018. Available online: http://folk.uio.no/ohammer/past/ (accessed on 5 May 2018).
14. Lyman, R. *Quantitative Paleozoology*; Cambridge University Press: Cambridge, UK, 2008.
15. Badgley, C. Counting individuals in mammalian fossil assemblages from fluvial environments. *Palaios* **1986**, *1*, 328–338. [CrossRef]
16. Koleff, P.; Gaston, K.J.; Lennon, J.J. Measuring beta diversity for presence—Absence data. *J. Anim. Ecol.* **2003**, *72*, 367–382. [CrossRef]
17. Lazaridis, G.; Kantiranis, N.; Ioakeimidis, I.; Bozukov, V. Excavations in the Early Villafranchian site Milia-5 (Grevena, Greece): A multidisciplinary approach. In *Abstract Book of the VIth International Conference on Mammoths and their Relatives, Grevena and Siatista, Greece, May 2014*; Scientific Annals; School of Geology, Aristotle University: Thessaloniki, Greece, 2014; Volume 102, p. 2.
18. Sepkoski, J.J. Alpha, beta, or gamma: Where does all the diversity go? *Paleobiology* **1988**, *14*, 221–234. [CrossRef] [PubMed]
19. Hammer, O.; Harper, D.A. *Paleontological Data Analysis*, 1st ed.; Blackwell Publishing: Hoboken, NJ, USA, 2006; pp. 1–351, ISBN-13 978-1-4051-1544-5.
20. Sabol, M. New findings of Late Pliocene vertebrates from Hajnácka I site (southern Slovakia). *Coloq. Paleontol.* **2003**, 595–602.
21. Guérin, C. Biozonation continentale du Plio- Pléistocène d'Europe et d'Asie occidentale par les mammifères: État de la question et incidence sur les limites Tertiaire/Quaternaire et Plio/Pléistocène. *Quaternaire* **2007**, *18*, 23–33. [CrossRef]